



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2020

The occurrence of *Eocnochelus* (Testudines, Pleurodira) from Sardinia supports palaeogeographic reconstruction of the proximity of the island to continental Western Europe during the Eocene

Georgalis, Georgios L ; Zoboli, Daniel ; Pérez-García, Adán ; Luigi Pillola, Gian ; Delfino, Massimo

Abstract: In this paper, we describe pleurodire turtle material from the island of Sardinia, Italy, originating from two Eocene localities of the Cixerri Formation. The more complete among the two specimens bears strong resemblance with the continental Western European *Eocnochelus eremberti* and is tentatively referred to the same species, while the second, less complete specimen is only provisionally referred to the genus *Eocnochelus*. The new Sardinian turtles add to the so far scarcely documented fossil record of pleurodires in Italy, while it ranks as among the very few Paleogene vertebrates known from the island. The identification of the widespread Eocene Western European genus *Eocnochelus* in the fossil record of Sardinia supports recent palaeogeographic reconstructions of the island, according to which the Sardinia-Corsica Massif was located rather close to mainland Europe and was subjected to a significant, counterclockwise rotation during the Paleogene.

DOI: <https://doi.org/10.13130/2039-4942/14443>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-191156>

Journal Article

Published Version



The following work is licensed under a Creative Commons: Attribution-NonCommercial-NoDerivatives 4.0 International (CC BY-NC-ND 4.0) License.

Originally published at:

Georgalis, Georgios L; Zoboli, Daniel; Pérez-García, Adán; Luigi Pillola, Gian; Delfino, Massimo (2020). The occurrence of *Eocnochelus* (Testudines, Pleurodira) from Sardinia supports palaeogeographic reconstruction of the proximity of the island to continental Western Europe during the Eocene. *Rivista Italiana di Paleontologia e Stratigrafia*:833-846.

DOI: <https://doi.org/10.13130/2039-4942/14443>

THE OCCURRENCE OF *EOCENOCHELUS* (TESTUDINES, PLEURODIRA) FROM SARDINIA SUPPORTS PALAEOGEOGRAPHIC RECONSTRUCTION OF THE PROXIMITY OF THE ISLAND TO CONTINENTAL WESTERN EUROPE DURING THE EOCENE

GEORGIOS L. GEORGALIS^{1,2,*}, DANIEL ZOBOLI³, ADÁN PÉREZ-GARCÍA⁴,
GIAN LUIGI PILLOLA³ & MASSIMO DELFINO^{2,5,*}

¹Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland

²Dipartimento di Scienze della Terra, Università di Torino, 35, via Valperga Caluso, 10125 Torino, Italy

³Dipartimento di Scienze Chimiche e Geologiche, Università di Cagliari, Cittadella Universitaria (Blocco A), 09042 Monserrato, Italy

⁴Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, Paseo Senda del Rey 9, 28040 Madrid, Spain

⁵Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA -ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain

*Corresponding authors: dimetrodon82@gmail.com; massimo.delfino@unito.it

To cite this article: Georgalis G.L., Zoboli D., Pérez-García A., Pillola G.L. & Delfino M. (2020) - The occurrence of *Eocenochelus* (Testudines, Pleurodira) from Sardinia supports palaeogeographic reconstruction of the proximity of the island to continental Western Europe during the Eocene. *Riv. It. Paleontol. Strat.*, 126(3): 833-846.

Keywords: Pleurodira; Testudines; Paleogene; biogeography; palaeogeography.

Abstract. In this paper, we describe pleurodire turtle material from the island of Sardinia, Italy, originating from two Eocene localities of the Cixerri Formation. The more complete among the two specimens bears strong resemblance with the continental Western European *Eocenochelus eremberti* and is tentatively referred to the same species, while the second, less complete specimen is only provisionally referred to the genus *Eocenochelus*. The new Sardinian turtles add to the so far scarcely documented fossil record of pleurodires in Italy, while it ranks as among the very few Paleogene vertebrates known from the island. The identification of the widespread Eocene Western European genus *Eocenochelus* in the fossil record of Sardinia supports recent palaeogeographic reconstructions of the island, according to which the Sardinia-Corsica Massif was located rather close to mainland Europe and was subjected to a significant, counterclockwise rotation during the Paleogene.

INTRODUCTION

Pleurodires are currently confined solely to the southern continents (Rhodin et al. 2017); however, this turtle clade achieved a significantly broader distribution during its Mesozoic and Cenozoic past (see Gaffney et al. 2006, 2011; Cadena 2015; Pérez-García et al. 2017b; Ferreira et al. 2018; Joyce &

Bandyopadhyay 2020), encompassing a diverse array of extinct taxa, also including *Stupendemys geographicus* Wood, 1976, one among the largest turtles of all time (Scheyer and Sánchez-Villagra 2007; Cadena et al. 2020). In Europe, pleurodires were one of the dominant and widespread turtle groups during the Late Cretaceous, but were also abundant and diverse during the Eocene (Owen & Bell 1849; Zigno 1889; Bergounioux 1954; Broin 1977; Kotsakis 1978; Lapparent de Broin 2003; Pérez-García et al. 2012, 2017a, 2017b, 2019; Rabi et al. 2012; Pérez-García &

Received: July 8, 2020; accepted: September 10, 2020

Lapparent de Broin 2013, 2015; Cadena 2015; Pérez-García 2016; Pérez-García & Chapman 2017; Pérez-García & Smith 2017). Their most recent records in this continent are from the early Neogene (Ristori 1895; Georgalis et al. 2013; Georgalis & Kear 2013). A number of Paleogene taxa from Western Europe have been identified as pertaining to the lineage of Erymnochelyinae, which is now represented by the extant taxon *Erymnochelys madagascariensis* (Grandidier, 1867), which is exclusive to Madagascar (Ferreira et al. 2018); nevertheless, Erymnochelyinae were once much more widespread during their Cenozoic past, distributed over Europe and Africa (Ferreira et al. 2018). Erymnochelyines were widespread in the Eocene of Central and Western Europe, achieving a diverse radiation comprising multiple species, pertaining to two genera, the freshwater *Neochelys* Bergounioux, 1954, and the littoral *Eocenochelys* Pérez-García, Lapparent de Broin & Murelaga, 2017b (Bergounioux 1954; Broin 1977; Pérez-García et al. 2017b). Despite their abundance and high levels of species diversity, European erymnochelyines became ultimately extinct at the end of the Eocene (Pérez-García et al. 2017b). Among European erymnochelyines, the genus *Eocenochelys*, species of which have been found across the Eocene of France, Spain, Belgium, and the United Kingdom, is the most phylogenetically proximate genus to the extant *Erymnochelys* Baur, 1888 (Pérez-García & Chapman 2017; Pérez-García & Smith 2017; Pérez-García et al. 2017b).

In Italy, the fossil record of pleurodire turtles has been so far limited to continental remains coming from the province of Veneto, in the northeastern part of the country. The remains from Veneto are represented by several specimens, including complete, articulated skeletons, and are already known since the late nineteenth century (Zigno 1889, 1890). They originate from two middle Eocene localities and have been originally referred to their own species: *Emys capellinii* Zigno, 1889 and *Neochelys bolcensis* Bergounioux, 1954 from the famous Lagerstätte of Monte Bolca, and *Emys nicolisii* Zigno, 1890 from Avesa (Zigno 1889, 1890). All of them seem to pertain to the podocnemidid erymnochelyine genus *Neochelys* (Bergounioux 1954; Broin 1977; Kotsakis 1978; Pérez-García & Lapparent de Broin 2015). *Neochelys capellinii* is in fact the type species of *Neochelys* and is currently almost universally considered a valid species (Lapparent de Broin 2003; Pérez-García & Lapparent de Broin 2013, 2015; Cadena 2015). *Neochelys bolcensis*

was initially introduced as *Platyarkia bolcensis* by Bergounioux (1953); however, he provided no description, definition, indication to a previous description, or figure of the material and as such, this 1953 binomen has to be considered a nomen nudum. *Neochelys bolcensis* was formally described by the same author the following year (Bergounioux 1954), but nevertheless, currently this taxon is considered to be a junior synonym of *N. capellinii* (e.g., Broin 1977). The validity of *Emys nicolisii* is at flux with the taxon likely representing a nomen dubium or at least a junior synonym of *N. capellinii*, though it has also been recently considered as a valid species as well, *Neochelys nicolisii* (Lapparent de Broin 2003; Pérez-García & Lapparent de Broin 2015; Lapparent de Broin 2018).

In a broader frame of a revision of the fossil turtles of Italy (Abbazzi et al. 2008; Chesi 2009; Chesi et al. 2007a, 2007b, 2009; Colombero et al. 2014, 2017; Cirilli et al. 2016; Georgalis et al. 2020), here we describe two shells of Eocene age from Sardinia, which are assigned to the genus *Eocenochelys*. We address their taxonomic affinities and compare them with other finds of the genus from continental Europe. Biogeographic implications of the new pleurodire remains are discussed, along with their impact on the palaeogeographic reconstruction of the Western Mediterranean during the Eocene.

MATERIAL AND METHODS

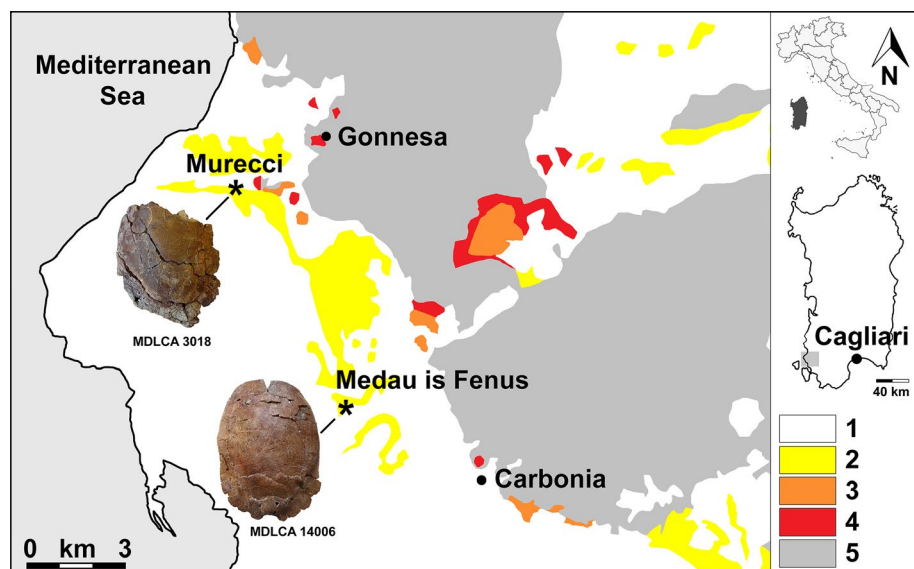
The fossil material described herein is curated at the collections of the MDLCA. The first of the two specimens (the most complete, MDLCA 14006) was briefly mentioned in abstracts and papers during the past two decades (Righi & Delfino 2003; Delfino & Rook 2008; Pérez-García & Chapman 2017; Pérez-García et al. 2017b); however, it has never been formally described or figured. The second one (MDLCA 3018) is presented here for the first time. Taxonomy follows Joyce et al. (2004) and Pérez-García et al. (2017b).

Institutional abbreviation. MDLCA, Museo Sardo di Geologia e Paleontologia “Domenico Lovisato”, University of Cagliari, Italy.

GEOLOGICAL SETTINGS

The turtle remains described herein originate from the Cixerri Formation, a continental succession cropping out discontinuously in southwestern Sardinia (Pecorini & Pomesano Cherchi 1969). The most complete specimen (MDLCA 14006) was collected in a sand quarry in the locality Medau is

Fig. 1 - Schematic geological map of the NW Sulcis Basin, Sardinia, showing also the position of the fossil localities which have provided the remains of turtles studied in this paper. 1) Undifferentiated Aquitanian–Holocene deposits; 2) Cixerri Formation (middle Lutetian–early Oligocene); 3) Lignitifero Formation (late Ypresian–early Lutetian); 4) Miliolitico Formation (early Ypresian); 5) Variscan metamorphic basement and Carboniferous–Mesozoic deposits.



Fenus, near Flumentepido (Municipality of Carbonia). The other specimen (MDLCA 3018) was collected in the locality of Murecchi (Municipality of Gonnese, Fig. 1). The geographic distance between these outcrops is around 7 km in straight line.

The Cixerri Formation is a terrigenous formation mainly represented by sandstones, subordinated siltites, and conglomerates with very rare intercalations of lignitiferous clays and lacustrine limestones (Pecorini & Pomesano Cherchi 1969; Barca & Costamagna 2010; Costamagna & Schäfer 2013). The conglomeratic levels are more frequent in the upper part of the succession. Generally, these are represented by rounded, polygenic and heterometric clasts originated from Paleozoic, Mesozoic and early Eocene lithotypes cropping out currently in the Sulcis-Iglesiente subregion. Furthermore, several authors reported the presence of pebbles with ?Aptian–Albian microfaunas originated from lithotypes of the Pyrenean domain, totally absent in the Sardinian area (Cherchi & Schroeder 1976; Cherchi 1979; Barca & Cherchi 2002). The Formation crops out extensively in southwestern Sardinia (Sulcis subregion) and in the Cixerri valley, with a maximum thickness of about 300 m (Pecorini & Pomesano Cherchi 1969; Funedda et al. 2009; Barca & Costamagna 2010). The nature of the sediments indicates a continental depositional context with a prevalence of fluvial facies (Pecorini & Pomesano Cherchi 1969). More precisely, the Cixerri Formation represents the molassic post-Pyrenean

phase sedimentation in Sardinia (Cherchi 1979; Barca & Costamagna 2010) and deposited in the middle to lower, distal part of a foreland alluvial plain fed by Iberian relieves (Costamagna & Schäfer 2013). Presently, only a portion of this alluvial plain is preserved, because a great part of this was cut in half by the following detachment of the Sardinia-Corsica Massif from the southern European margin (Costamagna & Schäfer 2013). Furthermore, Barca & Costamagna (2010) reported fluvial facies alternated with siliciclastic deposits containing marine ichnofacies and tidal stratal pattern in the Monastir area (Campidano di Cagliari subregion) suggesting at least temporary coastal/river mouth area. Marine influences are documented in eastern and southeastern Sardinia since the Thanetian (Matteucci 1985). However, the general trend in facies distribution during the Cixerri Formation time indicates a provenance of the sediments from the west to the east and suggests that the previous “short living” marine to lagoonal basin identified in the Sulcis area (starting with the ?late Thanetian, middle–late Ypresian “Calcarei a macroforaminiferi” Auct.), showing a clear transgression, running from the southwest to the east in the present day position, was bounded by emerged land towards the east and filled by continental deposits during the early Lutetian Lignitifero Auct Formation and Cixerri Formation molasse times. It is difficult to give more detailed palaeogeographical information, but the characters of the transgressive-regressive cycle and the tectono-sedimentary setting play in favor of a rel-

atively short time for the deposition of the Cixerri Formation. According to Barca & Costamagna (2010) and Costamagna & Schäfer (2013), the Cixerri Formation is settled in a more limited time span (middle Lutetian–early Rupelian). These authors used the presence of volcanoclastic pebbles at the top of the continental succession to discriminate another Formation (Flumentepido Formation; Barca & Costamagna 2010).

The Cixerri Formation rests conformably to unconformably over the late Ypresian–early Lutetian Lignitifero Formation or it is posed unconformably over the Variscan metamorphic basement (Costamagna & Schäfer 2013, and references therein). Upwards, it passes sharply through an unconformity to the calcalkaline volcanics of the Oligocene–Miocene cycle (about 22.8 ± 1.3 Ma) in the Sulcis area (Lecca et al. 1997) or to the terrigenous of the late Oligocene to Aquitanian Ussana Formation in the Campidano area (Pecorini & Pomesano Cherchi 1969). In addition, in the Cixerri Valley, the Cixerri Formation is clearly intruded by the Cenozoic volcanic rocks dated at 29.9–27.5 Ma (Savelli 1975; Savelli et al. 1979); more recently these rocks were recently dated to be 29.30 ± 1.2 to 26 Ma (Funedda et al. 2009).

The fossiliferous content of the Cixerri Formation is rather poor; in addition to the herein described turtle remains, only scarce plant remains (in particular palms), freshwater gastropods (*Lymnaea* cf. *orelongo*), and isolated bone fragments from lacustrine levels were reported from the Villamassargia, Gonnese, and Perdaxius areas (Taricco 1924; Maxia 1959).

Summarizing, the age of the Cixerri Formation is bracketed between the early Lutetian (which is the age at the top of the Lignitifero Formation) and the local first occurrence of intruded mid-late Rupelian volcanic products. According to these data, the turtle remains from the Cixerri Formation (sensu Barca & Costamagna 2010) can be referred to the middle Lutetian–early Rupelian; this time range slightly encompasses the so far known chronologic distribution of *Eocenchelus*, that is known exclusively up to the late Eocene. But, the reasons exposed above (tectono-sedimentary setting) suggest that the age of the Sardinian pleurodire remains is, in all likelihood, middle Eocene.

SYSTEMATIC PALAEONTOLOGY

Testudines Batsch, 1788

Pleurodira Cope, 1864

Pelomedusoides Cope, 1868

Podocnemididae Cope, 1868

Erymnochelyinae Broin, 1988 (sensu Pérez-García et al. 2017b)

Erymnochelyini Pérez-García, Díaz-Berenguer, Badiola & Canudo, 2019

Eocenchelus Pérez-García, Lapparent de Broin & Murelaga, 2017b

Eocenchelus eremberti (Broin, 1977)

Eocenchelus cf. *eremberti*

Figs. 2-3

Material: MDLCA 14006, an almost complete carapace and plastron, missing only tiny fragments of the anteriormost and posteriormost portions of the carapace (Fig. 2-3).

Locality: Medau is Fenus, near Flumentepido (Municipality of Carbonia), Sardinia; Cixerri Formation, probably middle Eocene.

Description. MDLCA 14006 is an almost complete shell, preserving most parts of the carapace and plastron (Figs. 2-3). The carapace misses only tiny fragments of the anteriormost and posteriormost portions, especially at the posterior right portion, near the marginals, as well as near the level of the first pleurals. Three prominent breakages are apparent on the carapace. Also, certain portions of the carapace are slightly deformed.

The carapace is oval, being 372 mm long and 306 mm wide (at mid-length and mid-width respectively). Its posterior part is relatively flattened dorsally; there are no signs of a medial or lateral keels. The posterior margin of the carapace is dorsally directed. It is not possible to determine whether a cervical scute was present (in the case of being present it should be extremely narrow, which is unlikely).

The limits between several plates are not clearly visible and these often coincide with the fractures. The plates of the carapace, which has been possible to identify, are represented by: a nuchal, six neurals, a suprapygal, a pygal, eight right and eight left costals, and at least nine right and nine or ten left peripherals. The nuchal is located immediately anterior to the neural series. It is covered by the vertebral I and the first pair of marginals. There are six neurals. The dimensions of all the neurals are

Fig. 2 - *Eocnochelus* cf. *eremberti* from Sardinia. MDLCA 14006, almost complete carapace and plastron. Photographs in dorsal (A), ventral (B), and left lateral (C) views.

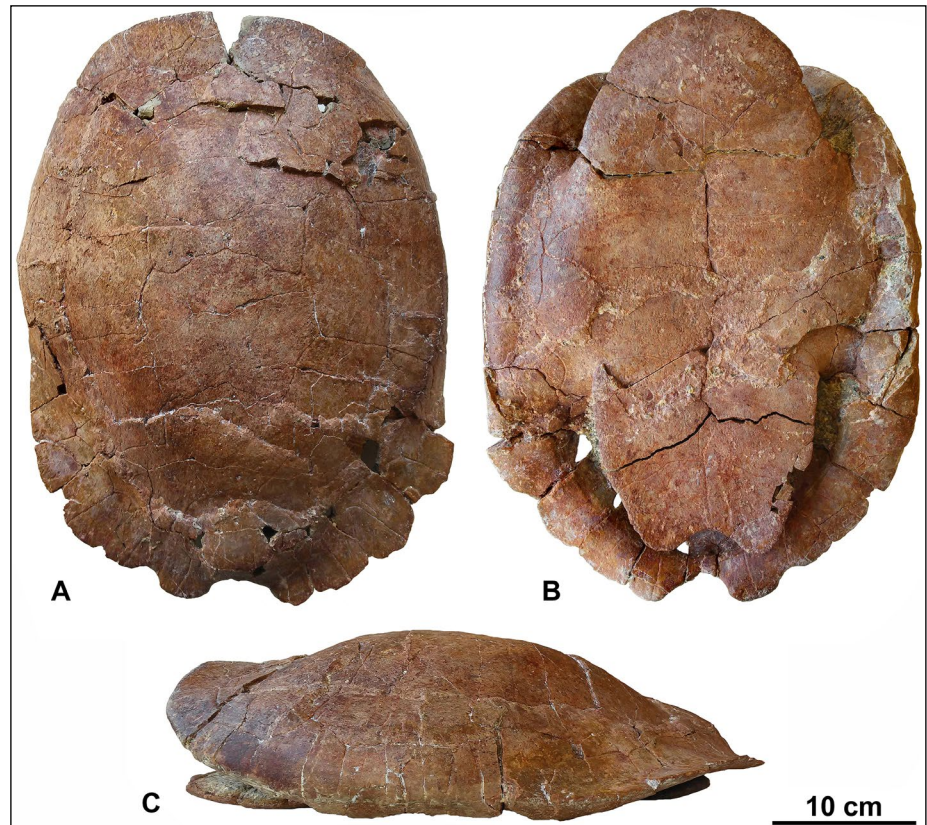
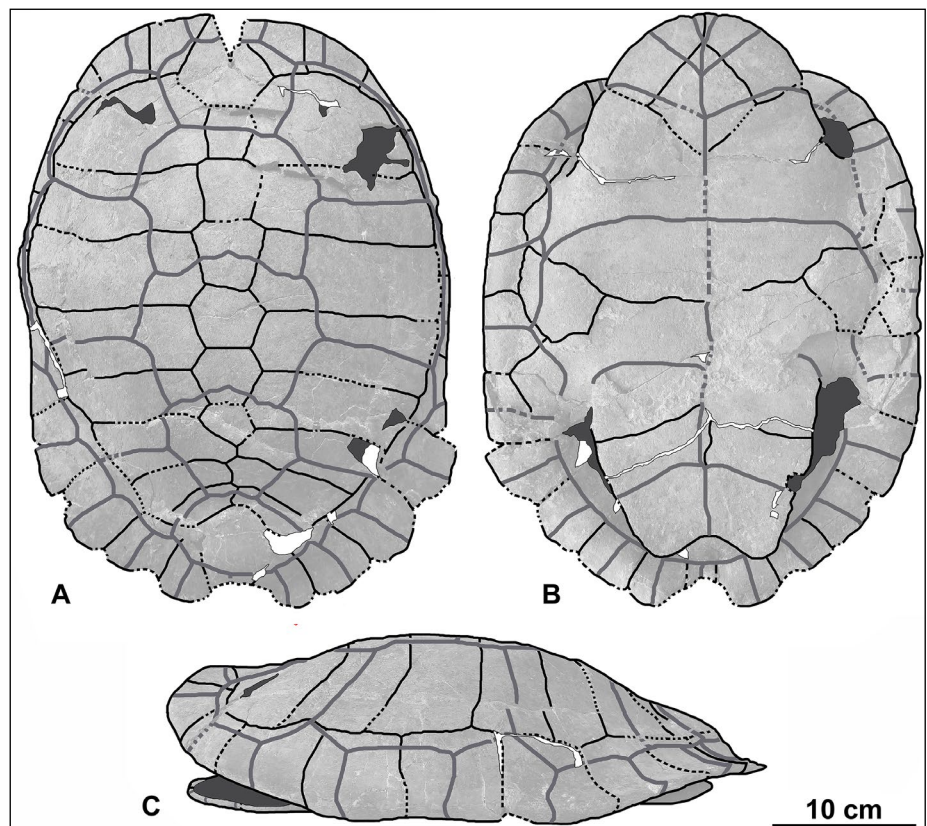


Fig. 3 - *Eocnochelus* cf. *eremberti* from Sardinia. MDLCA 14006, almost complete carapace and plastron. Interpretative drawings in dorsal (A), ventral (B), and left lateral (C) views.



more or less similar between them, with the exception of the last one, which has significantly smaller dimensions than the others. Their shape is hexago-

nal, with their smaller sides situated in their anterior positions and their formula is: 4-6a-6a-6a-6a-5. The last neural does not contact with the suprapygal,

due to the medial contact of the last three pairs of costals. The costals at the central area of the carapace are larger than laterally and they are decreasing both in width and height, towards both the anterior and posterior position in the series. Peripherals I-IX can be distinguished in the right series; the sutures of peripherals X and XI are hidden by fractures and areas in which shell portions are missing. From the left series, peripherals VII and VIII are not recognizable.

The remains of the scutes on the carapace afford some information about all the elements that originally constituted its external appearance. The scutes are represented by two series, each arranged on one side, of 12 marginals and four pleurals and by a single series of five vertebrals. The medial region of both first marginals is not preserved. The marginals II-VII have a rather similar shape and size between them, and are longer than wide. Among pleurals, pleural II is the largest, followed by pleurals I, III, and IV. The vertebrals II and III are the largest, both showing a similar size; they are followed in size by vertebrals I, IV, and V.

The plastron is 34.6 cm long and 26.4 cm wide (at the level of the mesoplastra). Its central part is slightly concave (it is unclear whether it is a product of deformation or if it was also the case of the specimen when in life). The anterior plastral lobe, 10.9 cm long, is rounded at the front and widens towards a posterior direction. Its outer edge folds slightly upwards. The posterior plastral lobe, 11.7 cm long, has an anal notch with an angle of 107°; its distal margin folds slightly upwards. The left bridge is 12.7 cm long. It is damaged by displaced fractures, in which the posterior area was collapsed. The right side bridge is well preserved, being 12.0 cm long. Several variably pronounced (and sometimes dislocated) fractures are visible, mainly with a transversal or oblique direction. In the plastron, the sulci that delimit the scutes are relatively evident, while several areas corresponding to the sutures between some plates are not clearly visible.

The plates in the plastron are represented by the entoplastron, the epiplastra, hyoplastra, mesoplastra, hypoplastra, and xiphiplastra. The entoplastron is of rhomboid shape and is located in the anterior portion of the plastron. The epiplastra are trapezoidal. The hyoplastra are longer than the hypoplastra. The mesoplastra are situated laterally, placed at the lateral limits of hyoplastra and hypoplastra.

Scutes are represented by a single gular and a pair of extragulars (sensu Hutchison & Bramble 1981), humerals, pectorals, abdominals, femorals, and anals. The element size formula of medial surface of the plastron is as follows: abdominals > pectorals > femorals > anals > gular \geq humerals > extragulars. The gular has small dimensions. The femorals have a trapezoidal shape and the sulcus with the anals is slightly posteriorly arched. The anals are rhomboid. Their posterior extremity is semioval and its margins form an angle of 107°.

cf. *Eocenochelus* sp.

Fig. 4

Material: MDLCA 3018, an incomplete carapace and plastron, missing the most of its anterior halves of both carapace and plastron (Fig. 4).

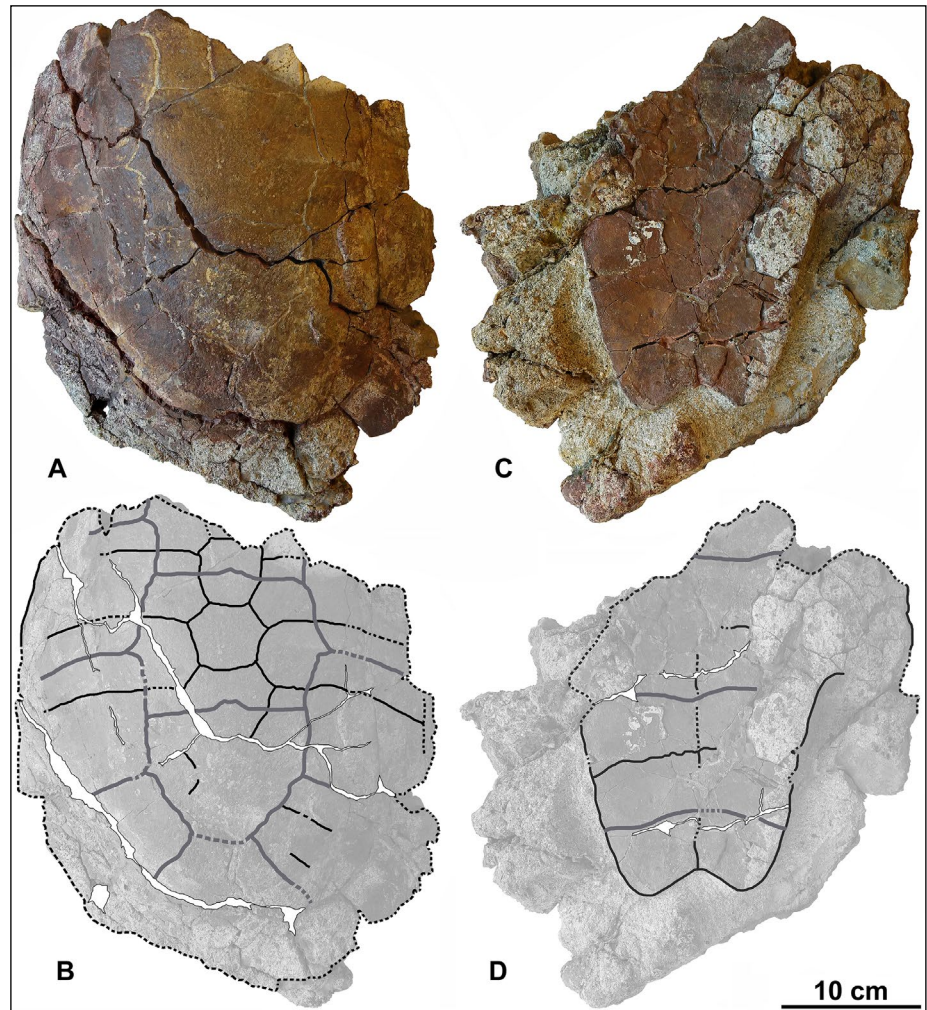
Locality: Murecci, (Municipality of Gonnese), Sardinia; Cixerri Formation, probably middle Eocene.

Description. MDLCA 3018 is a partial shell, lacking the anterior portion of both carapace and plastron (Fig. 4). The preserved portion of the shell is filled with matrix and is locally heavily fractured and incomplete. The surface is partly covered by a hard concretion. Therefore, most of the skeletal elements are not visible, though their presence can be supposed on the basis of the general shape of the shell. However, its morphology does not significantly differ from that of MDLCA 14006 and thus it will be only briefly commented here.

The carapace has a preserved midline length of 33.6 cm, while its maximum preserved width is 28.8 cm. The carapace preserves the neurals from the second (maybe a little portion of the second) to the last, but only the third, fourth and fifth can be seen with relative confidence (a posterolateral suture of the sixth could be present); the costals from the second to the last; the peripherals from the fourth to the last one. Pygal and suprapygal could be also present but this cannot be deciphered with certainty.

The plastron has a preserved midline length of 26.5 cm, while its maximum preserved width is 23.2 cm. The plastron preserves partial hyoplastra, the hypoplastra, and the xiphiplastra. The entire left mesoplastron and possibly part of the right mesoplastron are present but their sutures cannot be seen due to the presence of concretion and fractures.

Fig. 4 - cf. *Eocenocheilus* sp. from Sardinia. MDLCA 3018, incomplete carapace and plastron; photographs and interpretative drawings in dorsal (A, B), and ventral (C, D) views.



DISCUSSION

Taxonomic allocation

MDLCA 14006 can be identified as a member of Pleurodira considering characters as the present of a pair of laterally located mesoplastra, and that of a single gular. The absence of a trapezoidal anterior plastral margin allows to exclude its attribution to *Neochelys* (Pérez-García & Lapparent de Broin 2015), the only genus of Pleurodira that was hitherto identified in the fossil record of Italy (see Introduction above). The development of a long medial contact of the extragulars, due to the presence of a reduced gular, has been recognized as exclusive of Erymnochelyini (Pérez-García et al. 2017b, 2019). This specimen can be referred to the genus *Eocenocheilus* on the basis of the identification of an exclusive character combination within this clade including: absence of a medial keel on the carapace; vertebral I heptagonal, with short latero-anterior margins, and wider than the nuchal;

vertebral II approximately as wide as vertebral III, both scutes lacking wide lateral protrusions anterior to the limit between the pleural sulci; first pair of marginals overlapping no more than half of the length of the lateral nuchal margins; posterior plastral lobe narrower than the anterior one; absence of clear extragular protrusions; relatively long gular scute, reaching the anterior margin of the entoplastron or overlying its most anterior region; very short dorsal expansion of the plastral scute borders (see characters in Pérez-García et al. 2017b, 2019; Pérez-García & Smith 2017). Among *Eocenocheilus* spp., this Sardinian specimen shares several characters with the type species of the genus, *Eocenocheilus eremberti*, which constitute an exclusive combination for this form: sinuous lateral margins of the vertebral scutes; relatively long epiplastral symphysis, less than half the entoplastral length; relatively wide posterior plastral lobe; subrounded lateral margins of the posterior plastral lobe; relatively wide anal notch, its length being equivalent to half this width

or less (see Pérez-García et al. 2017b, 2019). It is worth noting that in terms of size, the Sardinian material approaches mostly the smallest species of the genus (i.e., *Eocnochelus lacombianus* Pérez-García, Lapparent de Broin & Murelaga, 2017b), which has a plastron length of around 30 cm and not respective elements of the largest species, *E. eremberti*, which reaches even around 50 cm in plastron length (see Pérez-García et al. 2017b, 2019). The presence of six neurals instead of seven differs from the known condition for the middle Eocene *E. eremberti*, being compatible with the one that characterizes the late Eocene *Eocnochelus farresi* Pérez-García, Lapparent de Broin & Murelaga, 2017b (Pérez-García et al. 2017b). However, other characters allow to exclude its attribution to this form (e.g., the combination of characters indicated as shared with *E. eremberti* as well as exclusive characters for *E. farresi*, such as the presence of a very short epiplastral symphysis, long lateral overlap of the humeral scutes onto hypoplastra, and an almost as long as wide U-shaped anal notch), as well as to the early Eocene *E. lacombianus* (e.g., the combination of characters indicated as shared with *E. eremberti* as well as the development of concave lateral margins of its notably narrow posterior plastral lobe, which represents an exclusive condition for *E. lacombianus*) (see Pérez-García et al. 2017b). The differences between the shell MDLCA 14006 and those hitherto known for *E. eremberti* cannot be ruled out as due different ontogenetic stages (e.g., the smaller size of the Sardinian specimen), and to an intraspecific variability for this species greater than that until now known (e.g., the difference in the number of neurals). Since other shell characters used for the characterization of *E. eremberti* (Pérez-García et al. 2017b, 2019; Pérez-García & Smith 2017) are unknown in MDLCA 14006, and also considering that the age of MDLCA 14006 cannot be confirmed as compatible with the known stratigraphic range of distribution for that species (Lutetian), we attribute MDLCA 14006 to *Eocnochelus* cf. *eremberti*.

Most of the characters available in the partial shell MDLCA 3018 are compatible with those observed in MDLCA 14006 (e.g., the morphology of the preserved neural plates and vertebral scutes; the width/length ratio of the anal notch and the morphology of its lateral margins), and the differences observed between them (e.g., the morphology of the posterior plastral lobe) are recognized

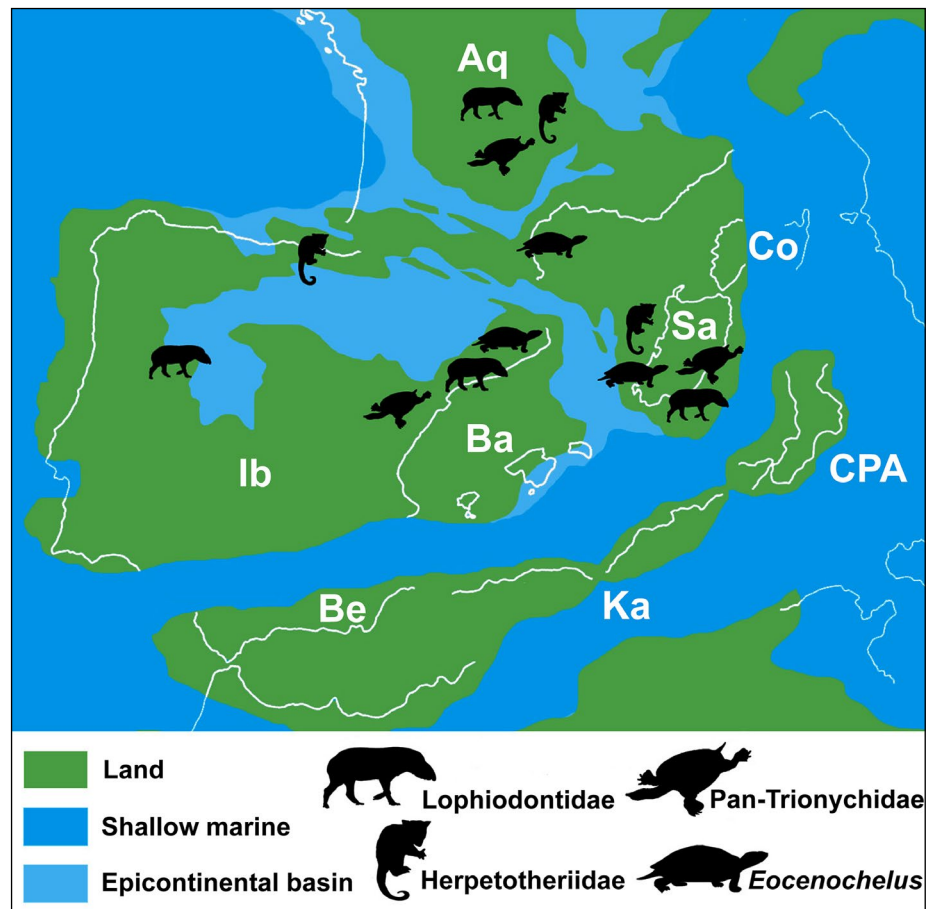
as compatible with the intraspecific variability observed in various members of Pleurodira, including *Eocnochelus eremberti* (Pérez-García & Smith 2017; Pérez-García et al. 2019). Despite the relative low number of characters provided by MDLCA 3018, it is attributed to cf. *Eocnochelus* sp. considering its potential compatibility with the same taxon represented by the almost complete Sardinian shell described above, as well as the fact that their remains are found in the same Formation and, in particular, in two localities that are situated relatively close to each other.

The well-preserved specimen (MDLCA 14006), comprising both carapace and plastron, ranks as one of the most complete shells of *Eocnochelus* known to date, being surpassed in completeness only by a recently described shell of *E. eremberti* from Spain (Pérez-García et al. 2019).

Palaeobiogeographic and palaeogeographic implications

The present identification of *Eocnochelus* in the Eocene of Sardinia provides interesting biogeographic implications. So far, Eocene tetrapods from Sardinia were represented by pan-trionychids, crocodylians, the marsupial *Amphiperatherium* Filhol, 1879, and the perissodactyls *Atalonodon monterini* Dal Piaz, 1929, and “*Lophiodon*” *sardus* Bosco, 1902 (Bosco 1902; Dal Piaz 1929; Kotsakis 1985; Kotsakis et al. 1997; Zoboli et al. 2019). With the exception of *Atalonodon monterini*, the crocodylians, and the pleurodire turtle material described herein, all tetrapod fossils come from the late Ypresian–early Lutetian Lignitifero Formation. The Eocene pan-trionychids from Sardinia are represented by indeterminate remains (Kotsakis 1985) that cannot be identified beyond the family level (Georgalis & Joyce 2017). The crocodylians are represented by a single small tooth from the Ypresian of Escalaplano (southeastern Sardinia) that cannot be taxonomically more precisely referred (Zoboli et al. 2019). The marsupial remains have not been yet formally described and were only provisionally referred to the genus *Amphiperatherium* (Kotsakis et al. 1997), a genus that is widespread in the Paleogene of continental Europe. “*Lophiodon*” *sardus* has been either referred to the lophiodontid genera *Lophiodon* Cuvier, 1822, and *Paralophiodon* Dedieu, 1977 (Bosco 1902; Esu & Kotsakis 1983; Palombo 2009), both genera that are widespread in the Paleogene of Europe, including

Fig. 5 - Palaeogeographic reconstruction of the Western Mediterranean during the Eocene, showing the position of the Sardinia-Corsica Massif. Silhouettes represent the shared continental tetrapod lineages that occurred in both areas during the late Ypresian–Lutetian. Abbreviations: Ba, Balearic Islands; Be, Betic; Ib, Iberia; Ka, Kabylia; CPA, Calabrian-Peloritan Arc; Sa, Sardinia; Co, Corsica; Aq, Aquitania. Map modified after Omodeo and Rota (2008) and Advokaat et al. (2014).



the Iberian Peninsula (Holbrook 2009). Anyway, a revision of the type material of “*L.*” *sardus* should be necessary to confirm the taxonomic position and validity of the taxon. However, the described fossil material of this perissodactyl is currently lost (Kotsakis et al. 2008). The other large mammal, *Atalonedon monterini*, was collected in the lithotypes of the Miliolitico Formation (early Ypresian) cropping out near the Terras de Collu coal mine (Gonnesa). *Atalonedon* is also currently considered a lophiodontid (e.g., Prothero & Schoch 1989; Holbrook 2009), whereas alternative relationships within perissodactyls have also been suggested (Palombo 2009); however, whether it indeed represents a Sardinian insular endemic genus or is instead referred to a mainland European one remains yet to be demonstrated.

The presence of related faunal elements among Sardinia and continental Western Europe should not appear at strange. Rather than that, current geodynamic reconstructions suggest that, during the early Paleogene, the Sardinia-Corsica Massif was rather close to continental Western Europe, with an important, about 45°, counter-clockwise rotation

subsequently taking place during the Eocene (Advokaat et al. 2014). Nevertheless, faunal distinction, at least to the species or even genus level, is the case for certain vertebrate taxa that occurred in the early Eocene of continental Western Europe and Sardinia, therefore implying the existence of some sort of temporary geographical or palaeoecological barriers between the Sardinia-Corsica Massif and the Iberian-Occitanian area that allowed endemic radiations flourishing in these nearby different landmasses during the late Paleocene–early Eocene time span (Matteucci et al. 2000; Palombo 2009). The rotation of the Sardinia-Corsica Massif continued also in post-Eocene times, as an even more prominent and well documented rotation (counter-clockwise of about 50°) took place, mostly during the early Miocene (Gattacceca et al. 2007); that being said, the total rotation of the Sardinia-Corsica Massif was of about 95° counterclockwise and was completed by around 15 Ma (Gattacceca et al. 2007). It is further worth noting that during the late Oligocene the Sardinia-Corsica Massif was still connected with the European mainland as documented by the presence of the continental ruminant “*Amphitragulus*” *quercyi*

(Mennecart et al. 2017) and early Miocene insular taxa with clear mainland affinities (de Bruijn & Rümke 1974; Van der Made 2008; Zoboli & Pillola 2017; Mennecart et al. 2019).

The new material described herein adds the pleurodire turtle *Eocnochelus* as another shared faunal element between Sardinia and continental Western Europe. Rather interestingly, in this case, such shared faunal resemblance reaches almost the species level, as the Sardinian material is identified as very close to *Eocnochelus eremberti*, if not conspecific. That species was originally established from the middle Eocene of northern France on the basis of both cranial and postcranial remains (Broin 1977), while additional, more or less coeval, material from Belgium (Pérez-García & Smith 2017) and Spain (Pérez-García et al. 2019) has recently been referred to it, demonstrating a rather broad geographic distribution during the middle Eocene. The other two named species of *Eocnochelus* are known from only from shell material from southern Europe and have much more confined geographic distributions, as only one specimen has been attributed to each of them so far: *Eocnochelus lacombianus* from the early Eocene of southwestern France, and *Eocnochelus farresi* from the late Eocene of northeastern Spain (Pérez-García et al. 2017b).

The new shell material from Sardinia allows the recognition of a form rather close to *Eocnochelus eremberti*. The depositional environment of the two Sardinian localities that yielded the new pleurodire remains indicates a freshwater environment (in which, *Eocnochelus*, adapted for life in littoral environments, would have arrived), demonstrating the non-marine nature of the sediments. Such close or even conspecific affinities between continental Western European coastal areas and Sardinian *Eocnochelus* do not necessitate direct land connection between these land masses in order to be explained. Instead, *Eocnochelus* has been suggested to be a taxon adapted for coastal habitats (Pérez-García et al. 2017b) and thus, even short marine distances between Western Europe and Sardinia during the Eocene would certainly not be a significant barrier for these pleurodires (see also Pérez-García & Chapman 2017). After all, pleurodires appear to have been rather capable of marine dispersals, with many taxa also inhabiting near shore environments (Sánchez-Villagra et al. 2000; Gaffney et al. 2006, 2011), with such dispersal events having

been repeatedly suggested for Cenozoic European taxa (Georgalis et al. 2013; Georgalis & Kear 2013; Pérez-García & Chapman 2017; Pérez-García et al. 2017b, 2019). The 95° counterclock-wise rotation of the Sardinia-Corsica Massif significantly shifted the position of the fossils of *Eocnochelus*, that have never lived in the central Tyrrhenian area, and therefore provides an interesting biogeographic case of “Viking funerary ship” (Mckenna 1973) in a Mediterranean setting. Finally, the occurrence of *Eocnochelus* in the Sardinian fossil record further adds to the growing evidence of the rich and diverse extinct reptilian fauna of the island that once comprised many different lineages that are currently globally extinct or extirpated from Europe (Portis 1901; Abbazzi et al. 2004, 2008; Venczel & Sanchíz 2006; Chesi et al. 2007a; Delfino et al. 2008, 2011; Georgalis et al. 2017, 2019; Tschopp et al. 2018; Zoboli et al. 2019).

CONCLUSIONS

The first pleurodire material from the island of Sardinia is described herein, comprising of two shells from two different, probably middle to late Eocene, localities. The most complete shell is referred to the erymnocelyine podocnemidid *Eocnochelus* cf. *eremberti*, while the incomplete specimen is only tentatively referred to as cf. *Eocnochelus* sp. Furthermore, the most complete Sardinian specimen represents one of the most complete known shells of the genus *Eocnochelus*, bearing more resemblance with the type species, *Eocnochelus eremberti*, fossils of which have also been found in Spain, France, and Belgium. The biogeographic importance of the new *Eocnochelus* remains is discussed, as these represent another shared related faunal element between Sardinia and continental Western Europe. Taking into consideration the former proximity of Sardinia with continental Western Europe and the rotation of the Sardinia-Corsica Massif from the Eocene onward, we envisage that *Eocnochelus* directly dispersed to Sardinia somewhen during the Eocene.

Acknowledgments. The shell MDLCA 14006 was prepared by F. Landucci (Department of Earth Sciences, University of Florence); D. Righi (University of Modena and Reggio Emilia) prepared its preliminary interpretative drawing and description in the frame of her master thesis. MD thanks H. Tong for her comments on MDLCA 14006 and for having suggested its erymnocelyine affinities. Project supported by Fondi di Ateneo dell'Università di Torino (2018-2019),

Generalitat de Catalunya (CERCA Program) and Spanish Agencia Estatal de Investigación (CGL2016-76431-P, AEI/FEDER, EU) to MD. GLG acknowledges support from a postdoctoral grant from the University of Torino and Forschungskredit of the University of Zurich, grant no. [FK-20-110]. DZ was supported by grants P.O.R. Sardegna F.S.E. 2014-2020 - Asse III "Istruzione e Formazione, Obiettivo Tematico: 10, Obiettivo Specifico: 10.5, Azione dell'accordo di Partenariato: 10.5.12 "Avviso di chiamata per il finanziamento di Progetti di ricerca - Anno 2017". APG acknowledges funding by the Ministerio de Ciencia e Innovación (PID2019-111488RB-I00). GLP research is supported by Fondi di Ateneo Cagliari University. GLP and DZ work was also supported by grants from Fondazione di Sardegna (grant number: F71/17000190002). The quality of the manuscript was improved by the useful comments of the reviewer Walter Joyce (University of Fribourg).

REFERENCES

- Abbazzi L., Angelone C., Arca M., Barisone G., Bedetti C., Delfino M., Kotsakis T., Marcolini F., Palombo M.R., Pavia M., Piras P., Rook L., Torre D., Tuveri C., Valli A. & Wilkens B. (2004) - Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, Eastern Sardinia, Italy), an overview. *Rivista Italiana di Paleontologia e Stratigrafia*, 110: 681-706.
- Abbazzi L., Carboni S., Delfino M., Gallai G., Lecca L. & Rook L. (2008) - Fossil vertebrates (Mammalia and Reptilia) from Capo Mannu Formation (Late Pliocene, Sardinia, Italy), with description of a new *Testudo* (Chelonii, Testudinidae) species. *Rivista Italiana di Paleontologia e Stratigrafia*, 114: 119-132.
- Advokaat E.L., van Hinsbergen D.J.J., Maffione M., Langeris C.G., Vissers R.L.M., Cherchi A., Schroeder R., Madani H. & Columbu S. (2014) - Eocene rotation of Sardinia, and the paleogeography of the western Mediterranean region. *Earth and Planetary Science Letters*, 401: 183-195.
- Agus M. & Pecorini G. (1978) - Livelli a carofite nel carbone della "prima vena" della miniera di Seruci e nel Cixerri. *Resoconti della Associazione Mineraria Sarda*, 84: 43-65.
- Barca S. & Cherchi A. (2002) - Introduction to the geology of Sardinia. In: Cherchi A., Corradini C. & Putzu M.T. (Eds.) - Sardinia field trip palaeontology & stratigraphy. 15° Convegno della Società Paleontologica Italiana, Sardinia, 8-14 October 2002. *Rendiconti della Società Paleontologica Italiana*, 1: 11-34.
- Barca S. & Costamagna L.G. (2010) - New stratigraphic and sedimentological investigations on the Middle Eocene-Early Miocene continental successions in South-western Sardinia (Italy): paleogeographic and geodynamic implications. *Comptes rendus Geoscience*, 342: 116-125.
- Batsch G.C. (1788) - Versuch einer Unleitung, zur Kenntniss und Geschichte der Thiere und mineralien. *Akademische Buchhandlung Jena*, 1: 1-528.
- Baur G. (1888) - Osteologische Notizen über Reptilien. Fortsetzung III, IV, V. *Zoologischer Anzeiger*, 11: 417-424.
- Bergounioux F.M. (1953) - Chéloniens fossiles des terrains tertiaires de la Vénétie. *Comptes Rendus de l'Académie des Sciences, Paris*, 236: 222-224.
- Bergounioux F.M. (1954) - Les Chéloniens fossiles des terrains tertiaires de la Vénétie. *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova*, 18: 1-115.
- Bosco C. (1902) - Il *Lophiodon sardus* (n. sp.) delle Lignite di Terras de Collu (Sardegna). *Rendiconti dell'Accademia dei Lincei*, 5: 178-182.
- Broin F. de. (1977) - Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mémoires du Muséum national d'histoire naturelle*, 38: 1-366.
- Broin F. de. (1988) - Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana et la dispersion géographique des tortues pleurodires à partir du Crétacé. *Studia Geologica Salmanticensia, Studia Palaeocheloniologica*, 2: 103-142.
- Cadena E. (2015) - A global phylogeny of Pelomedusoides turtles with new material of *Neochelys franzenii* Schleich, 1993 (Testudines, Podocnemididae) from the middle Eocene, Messel Pit, of Germany. *PeerJ*, 3: e1221.
- Cadena E.A., Scheyer T.M., Carrillo-Briceño J.D., Sánchez R., Aguilera-Socorro O.A., Vanegas A., Pardo M., Hansen D.M. & Sánchez-Villagra M.R. (2020) - The anatomy, paleobiology, and evolutionary relationships of the largest extinct side-necked turtle. *Science Advances*, 6: eaay4593.
- Carmignani L., Funedda A., Oggiano G. & Pasci S. (2004) - Tectono-sedimentary evolution of southwest Sardinia in the Paleogene: Pyrenaic or Apenninic Dynamic? *Geodinamica Acta*, 17: 275-287.
- Cherchi A. (1979) - Microfauna aptiano-(?) albiana dei ciottoli urgoniani della Formazione del Cixerri (Sardegna SW) e loro interesse paleogeografico. *Rivista Italiana di Paleontologia e Stratigrafia*, 85: 353-410.
- Cherchi A. & Montadert L. (1982) - The Oligo-Miocene rift of Sardinia and the early history of the western Mediterranean basin. *Nature*, 298: 736-739.
- Cherchi A. & Schroeder R. (1976) - Présence de galets du Vraconien supérieur-Cénomanien basal de provenance ibérique dans le Paléogène continental de Sud-Ouest de la Sardaigne. *Bull. Soc. Géol. France*, 18: 800-807.
- Chesi F. (2009) - Il registro fossile italiano dei cheloni [dissertation]. Università di Firenze, Florence, 178 pp.
- Chesi F., Delfino M., Abbazzi L., Carboni S., Lecca L. & Rook L. (2007a) - New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the central Mediterranean. *Rivista Italiana di Paleontologia e Stratigrafia*, 113: 287-297.
- Chesi F., Delfino M. & Rook L. (2009) - Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. *Journal of Paleontology*, 83: 379-388.
- Chesi F., Delfino M., Varola A. & Rook L. (2007b) - Fossil sea turtles (Chelonii, Dermochelyidae and Cheloniiidae) from the Miocene of Pietra Leccese (late Burdigalian-early Messinian), southern Italy. *Geodiversitas*, 29: 321-333.
- Cirilli O., Benvenuti M.G., Carnevale G., Casanovas Vilar I.,

- Delfino M., Furió M., Papini M., Villa A. & Rook L. (2016) - Fosso della Fittaia: the oldest Tusco-Sardinian late Miocene endemic vertebrate assemblages (Baccinello-Cinigiano Basin, Tuscany, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 122: 13-34.
- Colombero S., Alba D.M., D'Amico C., Delfino M., Esu D., Giuntelli P., Harzhauser M., Mazza P.P.A., Mosca M., Neubauer T.A., Pavia G., Pavia M., Villa A. & Carnevale G. (2017) - Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Palaeoecological and paleoclimatological implications. *Palaeontologia Electronica*, 20.1.10A: 1-66.
- Colombero S., Angelone C., Bonelli E., Carnevale G., Cavallo O., Delfino M., Giuntelli P., Mazza P., Pavia G., Pavia M. & Repetto G. (2014) - The Messinian vertebrate assemblages of Verduno (NW Italy): another brick for a latest Miocene bridge across the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 272: 287-234.
- Cope E.D. (1864) - On the limits and relations of the Raniformes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 16: 181-183.
- Cope E.D. (1868) - On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20: 242-300.
- Costamagna L.G. & Schäfer A. (2013) - The Cixerri Fm (Middle Eocene-Early Oligocene): analysis of a "Pyrenean" continental molassic system in southern Sardinia. *Journal of Mediterranean Earth Sciences Special Issue*, 2013: 41-44.
- Cuvier G. (1822) - Recherches sur les Ossements Fossiles (Nouvelle Edition), Volume 2, Part 1. Chez G. Dufour et E. D'Ocagne, Paris
- Dal Piaz G. (1929) - *Atalonodon*, nuovo genere di perissodattilo dell'Eocene di Gonnese (Sardegna). *Memorie dell'Istituto Geologico della Regia Università di Padova*, 8: 1-9.
- De Bruijn H. & Rümke C.G. (1974) - On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 77: 46-79.
- Dedieu P. (1977) - Sur la systematique des Tapiroidea (Mammalia) de l'Eocene européen. *Comptes rendus de l'Académie des Sciences, Série D*, 284: 2219-2222.
- Delfino M. & Bailon S. (2000). Early Pleistocene herpetofauna from Cava Dell' Erba and Cava Pirro (Apulia, Southern Italy). *Herpetological Journal*, 10: 95-110.
- Delfino M., Bailon S. & Pitruzzella G. (2011) - The late Pliocene amphibians and reptiles from "Capo Mannu D1 Local Fauna" (Mandriola, Sardinia, Italy). *Geodiversitas*, 33: 357-382.
- Delfino M., Kotsakis T., Arca M., Tuveri C., Pitruzzella G. & Rook L. (2008) - Agamid lizards from the Plio-Pleistocene of Sardinia (Italy) and an overview of the European fossil record of the family. *Geodiversitas*, 30: 641-656.
- Delfino M. & Rook L. (2008) - The fossil amphibians and reptiles of Sardinia: a summary. In: Corti C. (Ed.) - *Herpetologia Sardiniae*. Societas Herpetologica Italica. "Le Scienze", Edizioni Belvedere 8: 504.
- Esu D. & Kotsakis T. (1983) - Paleobiogeografia dei vertebrati e dei molluschi continentali del Terziario e del Quaternario della Sardegna. *Biogeographia - The Journal of Integrative Biogeography*, 8: 53-82.
- Ferreira G.S., Bronzati M., Langer M.C. & Sterli J. (2018) - Phylogeny, biogeography and diversification patterns of side-necked turtles (Testudines: Pleurodira). *Royal Society Open Science*, 5: 171773.
- Filhol H. (1879) - Etude des mammifères fossiles de Saint-Gérard-le-Puy. *Annales des Sciences Géologiques, Paris*, 10: 1-253.
- Funedda A., Carmignani L., Pasci S., Patta E.D., Uras V., Conti P. & Sale V. (2009) - Note Illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 556, Assemini. APAT - Dipartimento Difesa del Suolo-Servizio Geologico d'Italia, Roma, 182 pp.
- Gaffney E.S., Meylan P.A., Wood R.C., Simons E. & Campos D. de A. (2011) - Evolution of the side-necked turtles: the family Podocnemididae. *Bulletin of the American Museum of Natural History*, 350: 1-238.
- Gaffney E.S., Tong H. & Meylan P.A. (2006) - Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, 300: 1-700.
- Gattacceca J., Deino A.L., Rizzo R., Jones B., Henry B., Beaudoin B. & Vadeboin F. (2007) - Miocene rotation of Sardinia: new paleomagnetic and geochronological constraints and geodynamic implications. *Earth and Planetary Science Letters*, 258: 359-377.
- Georgalis G.L., Arca M., Rook L., Tuveri C. & Delfino M. (2019) - A new colubroid snake (Serpentes) from the early Pleistocene of Sardinia, Italy. *Bollettino della Società Paleontologica Italiana*, 58: 277-294.
- Georgalis G.L., Insacco G., Rook L., Spadola F. & Delfino M. (2020) - Turtle remains from the late Miocene of the Cessaniti area, southern Italy - insights for a probable Tortonian chelonian dispersal from Europe to Africa. *Swiss Journal of Palaeontology*, 139: 1.
- Georgalis G.L. & Joyce W.G. (2017) - A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. *Bulletin of Peabody Museum of Natural History*, 58: 115-208.
- Georgalis G.L. & Kear B.P. (2013) - The fossil turtles of Greece: an overview of taxonomy and distribution. *Geobios*, 46: 299-311.
- Georgalis G.L., Velitzelos E., Velitzelos D. & Kear B.P. (2013) - *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the Lower Miocene of Northern Greece. In: Brinkman D., Holroyd P., Gardner J., (Eds.) - *Morphology and evolution of turtles: papers in honor of Eugene S. Gaffney*. Volume 3. Pleurodires: 277-287, Springer, Dordrecht.
- Georgalis G.L., Zoboli D., Pillola G.L. & Delfino M. (2017) - A revision of the trionychid turtle *Procyclus sardus* Portis, 1901 from the late Miocene of Sardinia (Italy). *Annales de Paléontologie*, 103: 127-134.
- Grandidier A. (1867) - Liste des reptiles nouveaux découverts, en 1866, sur la côte sud-ouest de Madagascar. *Revue et Magazine de Zoologie, Paris, Série 2*, 19: 232-234.
- Holbrook L.T. (2009) - Osteology of *Lophiodon* Cuvier, 1822 (Mammalia, Perissodactyla) and its phylogenetic implications. *Journal of Vertebrate Paleontology*, 29: 212-230.

- Hutchison J.H. & Bramble D.M. (1981) - Homology of the plastral scales of the Kinosternidae and related turtles. *Herpetologica*, 37: 73-85.
- Joyce W.G. & Bandyopadhyay S. (2020) - A revision of the pelomedusoid turtle *Jainemys pisdurensis* from the Late Cretaceous (Maastrichtian) Lameta Formation of India. *PeerJ*, 8: e9330.
- Joyce W.G., Parham J.F. & Gauthier J.A. (2004) - Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, 78: 989-1013.
- Kotsakis T. (1978) - Sulle specie del genere *Neocheilus* Bergounioux (Testudinata, Pelomedusidae) dell'Eocene del Veneto. *Bollettino del Museo civico di storia naturale di Verona*, 5: 211-219.
- Kotsakis T. (1985) - Les Trionychidae (Testudinata, Reptilia) fossiles de l'Italie. *Bollettino della Società Paleontologica Italiana*, 24: 161-168.
- Kotsakis T., Barisone G. & Rook L. (1997) - Mammalian biochronology in an insular domain: the Italian Tertiary faunas. *Mémoires et Travaux de l'École Pratique des Hautes Études*, Institut de Montpellier, 21: 431-441.
- Kotsakis T., Murru M. & Palombo M.R. (2008) - Terras de Collu. EuroMam Fieldtrip Guide-Book, Sardinia, 16-21 September 2008. Publishedil Service, Cagliari, 98 pp.
- Lapparent de Broin F. de. (2003) - *Neocheilus* sp. (Chelonii, Erymnochelyinae), from Silveirinha, early Eocene, Portugal. *Ciências da Terra*, 15: 117-132.
- Lapparent de Broin F. de, Murelaga X., Pérez-García A., Far-rés F. & Altimiras J. (2018) - The turtles from the upper Eocene, Osona County (Ebro Basin, Catalonia, Spain): new material and its faunistic and environmental context. *Fossil Record*, 21: 237-284.
- Lecca L., Lonis R., Luxoro S., Melis E., Secchi F. & Brotzu P. (1997) - Oligo-Miocene volcanic sequences and rifting stages in Sardinia: a review. *Periodico di Mineralogia*, 66: 7-61.
- Matteucci R. (1985) - Marine Eocene of Sardinia. In: Cherchi A. (Ed.) - 19th European micropaleontological Colloquium. Sardinia October 1-10. Agip, Editar, Cagliari 1985: 80-86.
- Matteucci R., Caloi L., Murru M., Palombo M.R. & Raponi D. (2000) - Contesto paleoambientale dell'episodio carbonatico del miolotico Auct.nell'Eocene inferiore della Sardegna sudoccidentale. *Accademia Nazionale Scienze Lettere Arti di Modena, Collana di Studi*, 21: 161-168.
- Maxia C. (1959) - Malacofauna oligotipica di età paleogenica della Valle del Cixerri (Iglesiente). *Pubblico Istituto Geologico Paleontologico Università di Roma*, 95: 1-18.
- Mckenna M.C. (1973) - Sweepstakes, filters, corridors, Noah's Arks, and Beached Viking Funeral Ships in palaeogeography. In: Tarling D.H. & Runcorn S.K. (Eds.) - Implications of continental drift to the earth sciences: 295-308, Academic Press, New York.
- Mennecart B., Zoboli D., Costeur L. & Pillola G.L. (2017) - Reassessment of the latest Oligocene ruminant from Sardara, the last non-insular mammal from Sardinia (Italy). *Neues Jahrbuch für Geologie und Paläontologie*, 286: 97-104.
- Mennecart B., Zoboli D., Costeur L. & Pillola G.L. (2019) - On the systematic position of the oldest insular ruminant *Sardomeryx oschiriensis* (Mammalia, Ruminantia) and the early evolution of the Giraffomorpha. *Journal of Systematic Palaeontology*, 17: 691-704.
- Omodeo P. & Rota E. (2008) - Earthworm diversity and land evolution in three Mediterranean districts. *Proceedings of the California Academy of Sciences, Series 4*, 59: 65-83.
- Owen R. & Bell T. (1849) - Monograph on the fossil Reptilia of the London Clay, and on the Bracklesham and other Tertiary beds. Part I. Chelonia. *Paleontological Society Monograph*, 2: 1-76.
- Palombo M.R. (2009) - Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integrative Zoology*, 4: 367-386.
- Peconini G. & Pomesano Cherchi A. (1969) - Ricerche geologiche e biostratigrafiche sul Campidano meridionale (Sardegna). *Memorie della Società Geologica Italiana*, 8: 421-451.
- Pérez-García A. (2016) - A new turtle confirms the presence of Bothremydidae (Pleurodira) in the Cenozoic of Europe and expands the biostratigraphic range of Foxemydina. *The Science of Nature*, 103: 50.
- Pérez-García A., Antunes M.T., Barroso-Barcenilla F., Callapez P.M., Segura M., Soares A.F. & Torices A. (2017a) - A bothremydid from the middle Cenomanian of Portugal identified as one of the oldest pleurodiran turtles in Laurasia. *Cretaceous Research*, 78: 61-70.
- Pérez-García A. & Chapman S.D. (2017) - Identification of Podocnemididae (Pleurodira) in the British record by the first specimen of the coastal *Eocenocheilus* recognized outside Continental Europe. *Proceedings of the Geologists' Association*, 128: 757-763.
- Pérez-García A., Díaz-Berenguer E., Badiola A. & Canudo J.I. (2019) - An unexpected finding: identification of the first complete shell of the Franco-Belgian middle Eocene littoral pleurodiran turtle *Eocenocheilus eremberti* in Spain. *Historical Biology*, Published online: 18 Jul 2019.
- Pérez-García A. & Lapparent de Broin F. de. (2013) - A new species of *Neocheilus* (Chelonii, Podocnemididae) from the Ypresian (early Eocene) of the south of France. *Comptes Rendus Palevol*, 12: 269-277.
- Pérez-García A. & Lapparent de Broin F. de. (2015) - New insights into the anatomy and systematic of '*Papoulemys*' *laurenti*, a representative of *Neocheilus* (Chelonii, Podocnemididae) from the early Eocene of the south of France. *Paläontologische Zeitschrift*, 89: 901-923.
- Pérez-García A., Lapparent de Broin F. de & Murelaga X. (2017b) - The *Erymnochelys* group of turtles (Pleurodira, Podocnemididae) in the Eocene of Europe: new taxa and paleobiogeographical implications. *Palaeontologia Electronica*, 20.1.14A: 1-28.
- Pérez-García A., Ortega F. & Murelaga X. (2012) - A new genus of Bothremydidae (Chelonii, Pleurodira) in the Cretaceous of Southwestern Europe. *Geobios*, 45: 219-229.
- Pérez-García A. & Smith T. (2017) - Identification of the African-European *Erymnochelys* group (Pleurodira, Podoc-

- nemididae) in the Belgian fossil record: first finding of *Eocenochelus eremberti* outside its type locality. *Fossil Record*, 20: 245-251.
- Portis A. (1901) - Il *Procyclus sardus* Port., nuovo trionychide fossile della Sardegna. *Bollettino della Società Geologica Italiana*, 20: 51-79.
- Prothero D.R. & Schoch M.R. (1989) - Classification of the Perissodactyla. In: Prothero D.R. & Schoch R.M. (Eds.) - The evolution of Perissodactyla: 530-537, Oxford University Press, Oxford.
- Rabi M., Tong H. & Botfalvai G. (2012) - A new species of the side-necked turtle *Foxemys* (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Hungary and the historical biogeography of the Bothremydini. *Geological Magazine*, 149: 662-674.
- Rhodin A.G.J., Iverson J.B., Bour R., Fritz U., Georges A., Shaffer H.B. & van Dijk P.P. (2017) - Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. *Chelonian Research Monographs*, 7: 1-292.
- Rhodin A.G.J., van Dijk P.P., Iverson J.B. & Shaffer H.B. (2010) - Turtles of the world, 2010 update: Annotated checklist of taxonomy, synonymy, distribution and conservation status. *Chelonian Research Monographs*, 5: 1-136.
- Ristori G. (1895) - Di un nuovo Chelonio fossile del Miocene dell'Isola di Malta. *Atti della Società Toscana di Scienze Naturali, Memorie*, 14: 3-17.
- Sánchez-Villagra M.R., Burnham R.J., Campbell D.C., Feldmann R.M., Gaffney E.S., Kay R.F., Lozsan R., Purdy R. & Thewissen J.G.M. (2000) - A new near-shore marine fauna and flora from the Early Neogene of northwestern Venezuela. *Journal of Paleontology*, 74: 957-968.
- Savelli C. (1975) - Datazioni preliminaricol metodo K/Ar di vulcaniti della Sardegna sud-occidentale. In: Fornaseri M. (Ed.) - Società Italiana di Mineralogia e Petrologia; Atti della Riunione; tavola rotonda, Geochimica e geochimica isotopica. Editrice Succ. Fusi, Pavia.
- Savelli C., Beccaluva L., Deriu M., Macciotta G.P. & Maccioni L. (1979) - K/Ar Geochronology and evolution of the tertiary calco-alkaline volcanism of Sardinia (Italy). *Journal of Volcanology and Geothermal Research*, 5: 257-269.
- Scheyer T.M. & Sánchez-Villagra M.R. (2007) - Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: Phylogeny and function. *Acta Palaeontologica Polonica*, 52: 137-154.
- Taricco M. (1924) - Il bacino lignitifero di Gonnese (Provincia di Cagliari). *Bollettino del Regio Ufficio Geologico d'Italia*, 49: 1-14.
- Tschopp E., Villa A., Camaiti M., Ferro L., Tuveri C., Rook L., Arca M. & Delfino M. (2018) - The first fossils of *Timon* (Squamata: Lacertinae) from Sardinia (Italy) and potential causes for its local extinction in the Pleistocene. *Zoological Journal of the Linnean Society*, 184: 825-856.
- Van der Made J. (2008) - New endemic large mammals from the Lower Miocene of Oschiri (Sardinia): Observations on evolution in insular environment. *Quaternary International*, 182: 116-134.
- Venczel M. & Sanchíz B. (2006) - Lower Miocene Amphibians and Reptiles from Oschiri (Sardinia, Italy). *Hantkeniana*, 5: 72-75.
- Wood R.C. (1976) - *Stupendemys geographicus*, the world's largest turtle. *Breviora*, 436: 1-31.
- Zigno A. de. (1889) - Chelonii scoperti nei terreni cenozoici delle Prealpi Venete. Memoria. *Memorie Regio Istituto Veneto di Scienze*, 23: 119-130.
- Zigno A. de. (1890) - Chelonii terziari del Veneto. Memoria seconda: chelonio scoperto nel calcare nummulitico di Avesa presso Verona. *Letta al Reale Istituto Veneto di Scienze, Lettere ed Arti*, 1: 1-13.
- Zoboli D. & Pillola G.L. (2017) - Early Miocene insular vertebrates from Laerru (Sardinia, Italy): preliminary note. *Rivista Italiana di Paleontologia e Stratigrafia*, 123: 149-158.
- Zoboli D., Sanciù L., Pillola G.L. & Delfino M. (2019) - An overview of the crocodylian fossil record from Sardinia (Italy). *Annales de Paléontologie*, 105: 123-137.